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Biodiversity response to intensive biomass production from forest thinning in North American forests – A meta-analysis

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ABSTRACT

Demand for alternative energy sources has led to increased interest in intensive biomass production. When applied across a broad spatial extent, intensive biomass production in forests, which support a large proportion of biodiversity, may alter species composition, nutrient cycling and subsequently biodiversity. Because forest thinning and fuels treatment thinning are viewed as possible wide-spread biomass harvest options, it is important to understand what is known about forest biodiversity response to these practices and what additional information is needed by forest managers and policymakers. Therefore, we summarized documented relationships between forest thinning treatments and forest biodiversity from 505 biodiversity effect sizes (incl. taxa and guild abundance and species richness measures) from 33 studies conducted across North America. We used meta-analysis to summarize biodiversity response by region, taxa and harvest treatments. Biodiversity responses included species richness, diversity, abundance of taxa or groups of species (guilds) and abundance of individual species for birds, mammals, reptiles, amphibians, and invertebrates. Forest thinning treatments had generally positive or neutral effects on diversity and abundance across all taxa, although thinning intensity and the type of thinning conducted may at least partially drive the magnitude of response. Our review highlights the need for more research to determine effects of thinning on amphibians and reptiles and manipulative experiments designed to test the effects of biomass removal on biodiversity.

1. Background and definitions

Forest thinning is a silvicultural treatment that reduces tree density primarily to improve tree growth, to enhance forest health, or for economic reasons (Helms, 1998). Forests naturally thin through tree mortality resulting from competition in dense stands. Stands can be thinned before competitive self-thinning to meet economic objectives as well as objectives related to biodiversity conservation (Hayes et al., 1997, 2003; Carey and Wilson, 2001) and forest restoration (Hayes et al., 2003; Harrod et al., 2009). Wood products resulting from thinning operations are used in a variety of ways, although currently up to 60% of harvested material remains on-site (Parikka, 2004). An increase in availability of biofuels processing facilities may increase removal and use of thinned material (USDA Forest Service, 2005) which may partially offset harvest cost while meeting some of the increasing demand for biofuels (Page-Dumroese et al., 2010).

Thinning can increase structural complexity of young forests, subsequently increasing wildlife species diversity (Spies and Franklin, 1991; Hayes et al., 1997). Thinning produces a variety of short- and long-term changes to forest structure, the most obvious of which is a decrease in tree density and increase in forest canopy gaps and abundance and diversity of mid-story trees (Artman, 2003; Agee and Skinner, 2005; Hayes et al., 2003; Harrod et al., 2009). The more profound effect for wildlife species may be related to development of more complex understory vegetation due to increased light availability below the canopy (Doerr and Sandburg, 1986; Bailey and Tappeiner, 1998; Wilson and Carey, 2000; Garman, 2001; Homyack et al., 2005). Despite the favorable response of many species to thinning treatments, causal relationships between complexity of understory vegetation and increased species abundance or diversity have not been identified (Wilson et al., 2009). In addition, variable thinning intensities and harvest patterns (e.g. variable density thinning, clumped retention, or patch cuts) can produce favorable forest stand conditions for a variety of fauna (Carey and Wilson, 2001; Garman, 2001; Carey, 2003).

Thinning can be represented in three broad categories: precommercial thinning; commercial thinning; and fuels treatment

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thinning. The frequency with which each of these strategies is used across a landscape depends on landowner objectives, forest type, physiographic region, and other considerations. Often, a combination of these silvicultural treatments is used to achieve wood fiber, biodiversity, and forest health goals.

Managing regenerating stands often requires thinning of overstocked stands to maximize commercial harvest wood volume. Precommercial thinning (PCT) is the removal of trees, not for immediate financial return, but to reduce stocking density, allowing increased growth of more desirable crop trees (Helms, 1998). Precommercial thinning occurs early in stand development either before or just after canopy closure. The removal of sub-dominant sapling trees allows production of merchantable wood to increase substantially throughout the remainder of the rotation period (Reukema, 1975). Precommercial thinning is commonly used in the Northwest (especially in Douglas-fir forest types [Briggs, 2007]), increasingly used in Acadian forests of the Northeast (Homyack et al., 2007), decreasingly used on industrial forest lands in the Upper Midwest (D'Amato et al., 2008) and not common in commercial forests of the Southeast (Folegatti et al., 2007).

Commercial thinning is a partial-cutting process that produces merchantable material at least equal to the value of the direct costs of harvesting (Helms, 1998). Commercial thinning can occur at any time following canopy closure (Artman, 2003). Two-stage or multiple-entry overstory removal has been used to encourage understory development that simulates late seral forest characteristics at earlier ages (Thysell and Carey, 2001; Poage and Tappeiner, 2002; Hagar et al., 2004). However, few data have been presented to document the success of such techniques in producing the desired outcome (Lindh and Muir, 2004). The extent to which thinning of merchantable trees will be used for biofuels production is also unknown, and will likely depend heavily on fluctuating markets.

A fuels treatment is any manipulation or removal of wildland fuels to reduce likelihood of ignition or to lessen potential damage and resistance to control (Helms, 1998). As a result of decades of fire suppression efforts, fuels treatment forest thinning is increasingly used across the Western U.S. and Canada as a mechanism to reduce forest understory density and restore forest health (Agee and Skinner, 2005; USDA Forest Service, 2005). Mechanical thinning of understory vegetation is becoming commonplace in the dry forests of the Southwest (USDA Forest Service, 2005). Fuels treatments remove dense sapling trees and other woody understory vegetation to reduce ladder fuels that can lead to uncharacteristic stand-replacing wildfire (Agee and Skinner, 2005). However, depending on the length of time that fire has been suppressed from the stand, fuels treatment thinning can include thinning of merchantable trees to decrease crown density and add more wood volume to the timber sale (Skog and Barbour, 2006). As a result, the volume of wood removed in fuels treatment thinning is widely variable, and likely varies significantly by region and forest type. However, the total basal area removed is often less than for commercial and precommercial thinning treatments. Biomass removal as a fuels reduction treatment has been shown to be effective at decreasing near-term fire risk, but results may be mixed over longer time periods (Reinhardt et al., 2010).

Although pilot and experimental biomass harvests have been conducted across North America (Arnosti et al., 2008; Evans and Finkral, 2009), knowledge of how biodiversity responds to forest thinning is incomplete. Although the Southeastern U.S. is the leading timber-producing region of the United States (Prestemon and Abt, 2002), and thinning is a common silvicultural practice in all regions, most research on effects of thinning on wildlife species has been conducted in the Northwest. Reviews of forest thinning effects to date have been regional or local in geographic scope and primarily qualitative in their assessment (Hayes et al., 1997; Harrison, 1999; Muir et al., 2002; Thompson et al., 2003). However, detailed information about biodiversity response to forest thinning has recently been assessed quantitatively for the Southwestern United States (Kalies et al., 2010).

Most current research offers a snapshot assessment of the effect of forest thinning on species diversity and abundance. Effects of forest thinning operations on measures of diversity are often highly dependent on time since harvest, as many harvests will have a negative short-term effect on both species abundance and diversity (Wilson and Puettmann, 2007). The continent-wide meta-analytic approach we use to assess response of wildlife species diversity and abundance to different types of forest thinning represents a more comprehensive assessment of effects of biomass thinning harvests on terrestrial biodiversity across a variety of forest types and taxa.

2. Materials and methods

We reviewed the literature for papers that compared biodiversity responses to various thinning treatments. Definitions of biodiversity are wide ranging, and incorporate several scales of measurement. For the purpose of this work, biodiversity responses included species richness, diversity, abundance of taxa or groups of species (guilds) and abundance of individual species for birds, mammals, reptiles, amphibians, and invertebrates. We included both manipulative experiments (wildlife diversity and abundance measured before and after thinning treatments) and management experiments (stands paired post hoc and thinned areas are compared to unthinned controls). The controls presented were most commonly unthinned harvest-aged stands (30–75 yrs old). We included studies of precommercial, commercial, and fuels treatment thinning.

We used Wildlife and Ecology Worldwide, Web of Science, USDA Forest Service TreeSearch, and Google Scholar databases to search for relevant studies. We searched for the following forestry and biodiversity terms in article abstracts: thinning, precommercial thinning, selection harvest, fuels treatment, shelterwood, amphibian, avian, bird, mammal, reptile, invertebrate, insect, biodiversity, diversity, and richness. We supplemented searches by examining bibliographies of articles for additional references.

We found 33 studies ($k = 33$) relative to effects of forest thinning on wildlife species that provided control and treatment means, sample size and standard deviations for biodiversity responses, making them suitable for meta-analysis (Table 1). Several otherwise suitable studies did not report standard deviations or standard error measures. In some cases, the treatment and control means were provided with an associated two sample t-test statistic, p-value and degrees of freedom. When this occurred, we used the pooled variance in place of individual treatment and control standard deviation measures. When neither standard deviation nor test-statistic/p-values were reported, we contacted the authors and, when the data were available, we calculated error values from the raw data. If error measures could not be back-calculated and the raw data were not available, we did not include the study in analyses, but did include them in the discussion. When studies presented comparisons for a metric in consecutive years, we calculated overall mean effect and standard deviation using the pooled variance.

Because responses to habitat manipulations can vary greatly among taxa and among species within taxa, we considered different biodiversity measures (e.g., diversity, guild abundance, species abundance) from the same study to be independent effects (Bender et al., 1998). For birds, we also calculated 2 separate measures of effect size for species measured in summer and winter, because behavior, habitat requirements, and composition of bird communities often differs during those 2 seasons.

Table 1
Summary of manipulative studies used in meta-analysis.

Study	Location	Forest type	Taxa	Effect sizes[a]	Thinning intensity[b]	Commercial thin?	Fuel treatment thin?	Data collection
Amacher et al. (2008)	California	Mixed conifer	Mammals	0,0,0,4	Light	Y	Y	1 yr post-treatment
Artman (2003)	Washington	Hemlock/Douglas fir	Breeding birds	0,0,3,11	Moderate	Y	N	3–5 yrs post-treatment
Carey and Wilson (2001)	Washington	Hemlock/Douglas fir	Mammals	0,0,0,7	Light	Y	N	1–4 years post-treatment
Dellasala et al. (1996) A	SE Alaska	Hemlock/Douglas fir	Breeding birds	1,1,0,15	Moderate	N (PCT)	N	3–5 yrs post-treatment
Dellasala et al. (1996) B	SE Alaska	Hemlock/Douglas fir	Winter birds	1,1,0,3	Moderate	N (PCT)	N	3–5 yrs post-treatment
Easton and Martin (1998)	British Columbia	Cedar/Hemlock	Breeding birds	0,1,11,0	Light	N (understory)	N	1–3 yrs post-treatment
Ford et al. (2000)	North Carolina	Appalachian N. Red Oak	Amphibians and mammals	0,0,0,10	Heavy	Y	N	2 years post-treatment
Garman (2001) A	Oregon	Hemlock/Douglas fir	Amphibians and mammals	1,1,1,10	Moderate	N (PCT)	N	5, 6 and 8 years post-treatment
Garman (2001) B	Oregon	Hemlock/Douglas fir	Amphibians and mammals	1,1,1,10	Heavy	N (PCT)	N	5, 6 and 8 years post-treatment
Greenberg et al. (2007a,b)	North Carolina	Oak-Hickory hardwood	Birds and mammals	0,0,1,18	Light	N (understory)	Y	1–4 years post-treatment
Hagar et al. (1996) A	Oregon	Hemlock/Douglas fir	Breeding birds	1,1,0,20	Light	Y	N	5–15 years post-treatment
Hagar et al. (1996) B	Oregon	Hemlock/Douglas fir	Winter birds	1,1,0,6	Light	Y	N	5–15 years post-treatment
Hagar et al. (2004) A	Oregon	Hemlock/Douglas fir	Breeding birds	1,1,0,24	Moderate	N (PCT)	N	1–4 years post-treatment
Hagar et al. (2004) B	Oregon	Hemlock/Douglas fir	Breeding birds	1,1,0,25	Heavy	N (PCT)	N	1–4 years post-treatment
Homyack et al. (2005)	Maine	Acadian	Mammals	0,0,0,4	Light	N (PCT)	N	1–17 years post-treatment
Hurteau et al. (2008)	Arizona	Ponderosa pine	Breeding birds	1,0,0,5	Moderate	N (understory)	Y	2–4 years post-treatment
Kilpatrick et al. (2004)	South Carolina	Southern pine	Amphibians and reptiles	1,1,0,9	Light	N (understory)	Y	1–2 years post-treatment
Klenner and Sullivan (2003)	British Columbia	Subalpine spruce-fir	Mammals	0,0,0,4	Light	Y	N	1–3 yrs post-treatment
Larson (2001) A	Oregon	Hemlock/Douglas fir	Mammals	0,0,0,10	Moderate	Y	N	4–6 years post-treatment
Larson (2001) B	Oregon	Hemlock/Douglas fir	Mammals	0,0,0,10	Heavy	Y	N	4–6 years post-treatment
Loeb and Waldrop (2008)	South Carolina	Southern pine	Mammals	0,1,0,3	Light	N (understory)	Y	1–2 years post-treatment
Matthews et al. (2010)	North Carolina	Mixed Oak-Hickory-Pine	Amphibians and reptiles	2,2,5,4	Light	N (understory)	Y	3 years post-treatment
Norton and Hannon (1997) A	Alberta	Aspen	Breeding birds	0,0,6,0	Moderate	Y	N	1–2 years post-treatment
Norton and Hannon (1997) B	Alberta	Aspen	Breeding birds	0,0,6,0	Heavy	Y	N	1–2 years post-treatment
Perry and Thill (2005)	Arkansas	Mixed pine-hardwood	Mammals	0,1,0,5	Moderate	Y	N	1.5–5.5 years post-treatment
Ransome et al. (2004) A	British Columbia	Lodgepole pine	Mammals	0,0,0,2	Moderate	N (PCT)	N	12–14 years post-treatment
Ransome et al. (2004) B	British Columbia	Lodgepole pine	Mammals	0,0,0,4	Heavy	N (PCT)	N	12–14 years post-treatment
Siegel and DeSante (2003)	California	Mixed conifer	Breeding birds	0,1,4,35	Moderate	Y	Y	5–8 years post-treatment
Sullivan et al. (2005) A	British Columbia	Lodgepole pine	Mammals	2,1,0,3	Moderate	N (PCT)	N	12–14 years post-treatment
Sullivan et al. (2005) B	British Columbia	Lodgepole pine	Mammals	4,2,0,6	Heavy	N (PCT)	N	12–14 years post-treatment
Sullivan et al. (2007) A	British Columbia	Lodgepole pine	Mammals	0,0,0,3	Moderate	N (PCT)	N	12–15 years post-treatment
Sullivan et al. (2007) B	British Columbia	Lodgepole pine	Mammals	0,0,0,6	Heavy	N (PCT)	N	12–15 years post-treatment
Suzuki (2001)	Oregon	Hemlock/Douglas fir	Amphibians and mammals	0,2,0,14	Moderate	N (PCT)	N	1–2 years post-treatment
Suzuki and Hayes (2003)	Oregon	Hemlock/Douglas fir	Mammals	0,1,0,8	Light	N (PCT)	N	7–24 years post-treatment
Tibbels and Kurta (2003)	Michigan	Red pine	Insects and mammals	0,2,4,0	Moderate	Y	N	5–11 years post-treatment
Todd and Andrews (2008)	South Carolina	Coastal pine plantation	Reptiles	0,0,0,2	Light	Y	N	0.5–2.5 years post-treatment
Twedt and Somershoe (2009)	Louisiana	Bottomland hardwood	Breeding birds	0,0,0,14	Light	Y	N	1-12 years post-treatment
Wampler et al. (2008) A	New Mexico	Mixed conifer	Mammals	1,1,0,3	Light	N (understory)	Y	2–3 years post treatment
Wampler et al. (2008) B	New Mexico	Mixed conifer	Mammals	1,1,0,3	Moderate	Y	Y	2–3 years post treatment
Welsh et al. (1992)	Massachusetts	Massachusetts oak	Breeding birds	0,0,3,9	Light	N (cordwood)	N	1–10 years post treatment
Wilson et al. (1995)	Arkansas	Pine grassland	Breeding birds	1,0,0,23	Light	N (WSI)	Y	1–2 years post-treatment
Yi (2007) A	Oregon	Hemlock/Douglas fir	Insects	2,0,19,0	Moderate	Y	N	4–5 years post-treatment
Yi (2007) B	Oregon	Hemlock/Douglas fir	Insects	2,0,18,0	Heavy	Y	N	4–5 years post-treatment
Zebehazy et al. (2004) A	South Carolina	Southern pine	Breeding birds	1,1,0,11	Light	N (understory)	Y	1–2 years post-treatment
Zebehazy et al. (2004) B	South Carolina	Southern pine	Winter birds	1,1,0,7	Light	N (understory)	Y	1–2 years post-treatment

[a] Numbers indicate effect sizes for diversity/richness, total taxa abundance, guild abundance and species abundance respectively.
[b] Determined by the percent of unthinned (control) stand basal area or trees per hectare remaining in thinned (treatment) stands (heavy: 0–33; moderate: 34–66; light: 67–100).

When studies presented comparisons in different intensities of thinning, we similarly treated these as separate experiments because species' responses can vary among these treatments. However, many studies reporting results from different thinning intensities used the same control stands to compare each thinning intensity. To account for this lack of independence, we conducted meta-analysis for each taxon across all thinning intensities and separately for each thinning intensity. Because we considered myriad forest types with different potential stocking densities, we determined thinning intensity by calculating percent of unthinned (control) stand basal area or trees per hectare remaining in thinned (treatment) stands and categorized them as heavy (0–33%), moderate (34–66%), or light thins (67–100%). In addition, we calculated the average timing of data collection (years post-treatment) for each taxa.

Of the 33 studies we selected, 19 were manipulative experiments and 14 were management experiments. The literature included 11 precommercial thinning, 12 commercial thinning, and 10 fuels treatment studies, resulting in 505 individual effects sizes (Table 1). None of the studies reviewed were specifically designed to test thinning as a biomass removal technique. However, precommercial, commercial and fuels-treatment thinning are possible mechanisms for biomass harvest. As a result, we included all types of thinning in a cumulative meta-analysis. In addition, we analyzed fuels treatment studies separately because that technique is more likely to be used for stand restoration than for commercial harvest. Most studies were from the Northwest region (16), with fewer in other regions (Southeast [10]; Southwest [4]; Northeast [3]; Fig. 1).

We conducted all meta-analyses using Meta-Win software (Rosenberg et al., 2000). For each of the 505 responses, we calculated a response ratio which is the ratio of the experimental to control groups (Hedges et al., 1999). For each response, we treated non-thinned stands as the control. Thus, response ratios < 1.00 indicate a negative response to forest thinning, and ratios > 1.00 indicate a positive response to forest thinning. Because some means were zero, we added 1 to all means before calculating effect sizes. We used bootstrap confidence intervals and considered a combined effect to be significant if the confidence interval did not include 1.00. Some meta-analyses are based on multiple effect sizes originating from only 1 or 2 studies. Following the suggestions of Borenstein et al. (2009, p. 364), we do report meta-analysis results in such situations but also provide limitations for its application.

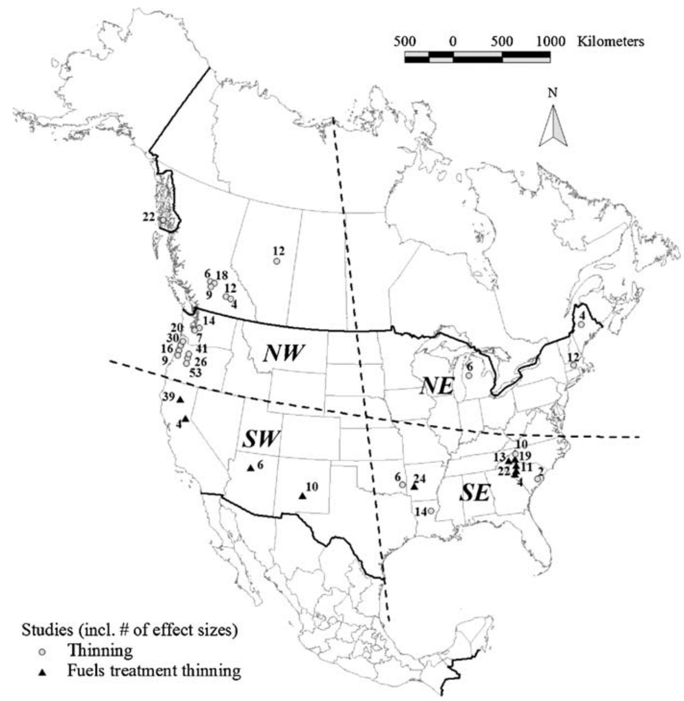

Fig. 1. Distribution of effects sizes in North America.

3. Response of birds to forest thinning

3.1. Results of breeding and wintering bird species meta-analysis

We found 274 bird responses (effect sizes) from 13 studies involving comparisons of thinned and unthinned forest stands with a significant cumulative effect size of 1.11 (Table 1; Fig. 2). This was nearly double the number of effect sizes for the next most commonly reported taxon (mammals; $n = 149$), but the effect sizes came from fewer studies ($k = 13$ for birds; $k = 17$ for mammals). Despite the large number of effect sizes, most were for abundance measures of individual bird species, leaving a limited number of measures of taxa/guild abundance and diversity to draw conclusions through meta-analysis. The hairy woodpecker (*Picoides villosus*) was the

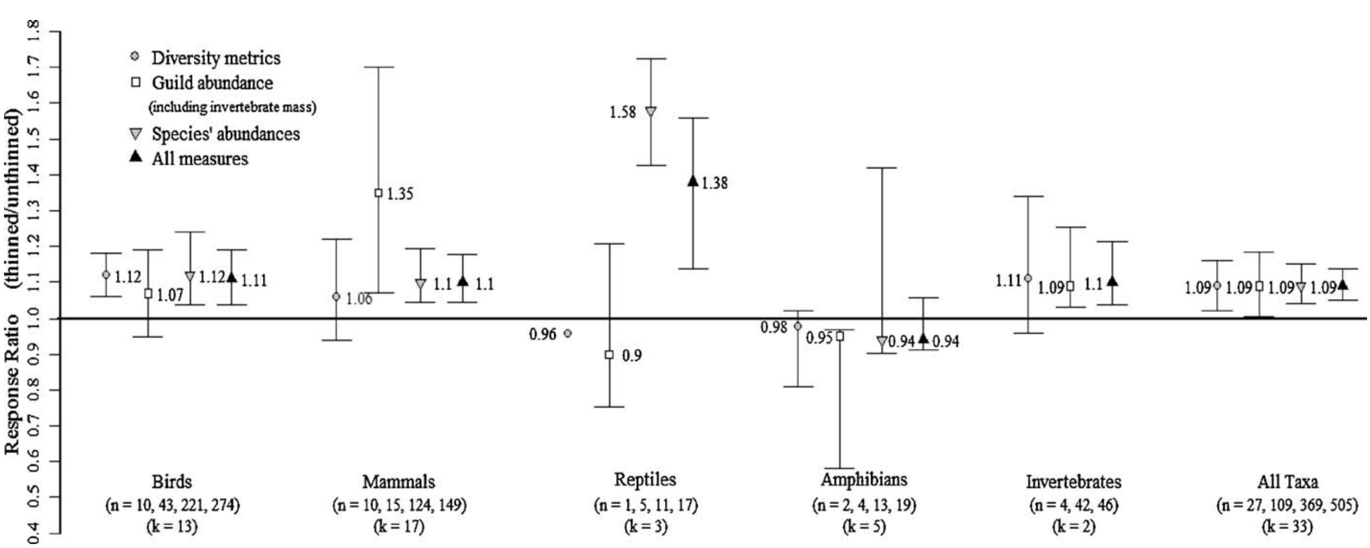

Fig. 2. Summary effect sizes for birds, mammals, amphibians and invertebrates across all manipulations. Means plotted without confidence intervals represent only one effect size ($n = 1$).

Table 2
Summary of effects of forest thinning on biodiversity by taxa and region.

	Northwest	Southwest	Southeast	Northeast	All regions
Birds	$k=6$	$k=2$	$k=4$	$k=1$	$k=13$
Diversity	1.15 ($n=6$)[a]	0.90 ($n=1$)	1.08 ($n=3$)	–	1.12 ($n=10$)[a]
Taxa/guild abundance	0.98 ($n=33$)	1.48 ($n=5$)[a]	1.14 ($n=2$)[a]	1.20 ($n=3$)[a]	1.07 ($n=43$)
Species abundance	1.03 ($n=104$)	1.23 ($n=39$)[a]	1.08 ($n=69$)	1.04 ($n=9$)	1.12 ($n=221$)[a]
Cumulative	1.02 ($n=143$)	1.27 ($n=45$)[a]	1.08 ($n=74$)	1.08 ($n=12$)	1.11 ($n=274$)[a]
Mammals	$k=9$	$k=2$	$k=4$	$k=2$	$k=17$
Diversity	0.98 ($n=8$)	1.52 ($n=2$)[a]	–	–	1.06 ($n=10$)
Taxa/guild abundance	0.99 ($n=9$)	1.90 ($n=2$)[a]	2.56 ($n=3$)[a]	1.54 ($n=1$)	1.35 ($n=15$)[a]
Species abundance	1.03 ($n=91$)	1.69 ($n=10$)[a]	1.37 ($n=19$)[a]	1.91 ($n=4$)[a]	1.10 ($n=124$)[a]
Cumulative	1.02 ($n=108$)	1.67 ($n=14$)[a]	1.44 ($n=22$)[a]	1.86 ($n=5$)[a]	1.10 ($n=149$)[a]
Reptiles			$k=3$		$k=3$
Diversity			0.96 ($n=1$)		0.96 ($n=1$)
Taxa/guild abundance	–	–	0.90 ($n=5$)	–	0.90 ($n=5$)
Species abundance			1.58 ($n=11$)[a]		1.58 ($n=11$)[a]
Cumulative			1.38 ($n=17$)[a]		1.38 ($n=17$)[a]
Amphibians	$k=2$		$k=3$		$k=5$
Diversity	–		0.98 ($n=2$)		0.98 ($n=2$)
Taxa/guild abundance	0.96 ($n=1$)	–	0.61 ($n=3$)[a]	–	0.95 ($n=4$)[a]
Species abundance	1.19 ($n=6$)		0.87 ($n=7$)		0.94 ($n=13$)
Cumulative	1.15 ($n=7$)		0.92 ($n=12$)		0.94 ($n=19$)
Invertebrates	$k=1$			$k=1$	$k=2$
Diversity	1.11 ($n=4$)			–	1.11 ($n=4$)
Order/guild biomass	1.19 ($n=37$)[a]	–	–	1.02 ($n=5$)	1.09 ($n=42$)[a]
Species biomass	–			–	–
Cumulative	1.15 ($n=41$)[a]			1.02 ($n=5$)	1.10 ($n=46$)[a]
All taxa combined	$k=16$	$k=4$	$k=10$	$k=3$	$k=33$
Diversity	1.07 ($n=18$)	1.34 ($n=3$)[a]	1.06 ($n=6$)	–	1.09 ($n=27$)[a]
Taxa/guild abundance	1.01 ($n=80$)	1.52 ($n=7$)[a]	1.42 ($n=13$)	1.06 ($n=9$)[a]	1.09 ($n=109$)
Species abundance	1.03 ($n=201$)	1.26 ($n=49$)[a]	1.10 ($n=106$)	1.16 ($n=13$)	1.09 ($n=369$)[a]
Cumulative	1.03 ($n=299$)	1.30 ($n=59$)[a]	1.11 ($n=125$)[a]	1.10 ($n=22$)[a]	1.09 ($n=505$)[a]

[a] Indicates bootstrap confidence intervals (1000 iterations) did not include 1.00; k = # of studies, n = # of effect sizes.

most commonly reported individual species ($k=6$) with a significant cumulative effect size of 1.28.

Most effect sizes (52%) were from the Northwest (Table 2; Fig. 1). However, studies from the Northwest represented a variety of forest types (e.g. lodgepole, aspen, coastal hemlock/fir, interior hemlock/cedar and mixed conifer). The average timing of data collection from the 13 studies was 3.81 (±0.69) years post-thinning treatment. Response data were collected between 1 and 15 years post-treatment, but only 3 studies (Hagar et al., 1996; Siegel and DeSante, 2003; Twedt and Somershoe, 2009) investigated response to thinning beyond 5 years post-treatment. Bird communities consistently responded favorably to forest thinning treatments overall (Fig. 2). Across all regions and treatments, effects were significantly greater than 1.00 for all diversity and abundance measures except taxa/guild abundance (Table 2; Fig. 2). Magnitudes of effects were generally comparable for birds and all other taxa (Fig. 2). Studies from the Southwest reported significantly positive effects of thinning treatments on guild and species abundance but cumulative effect sizes for diversity measures were not significantly different from 1 ($k=2$). Thinning also proved to be a positive influence on bird species diversity measures in the Northwest, and bird taxa/guild abundance measures in the Southeast and Northeast (Table 2). Thinning intensity played a significant role in bird response. Birds responded favorably to light and moderate thinning (Table 3). Heavy thinning led to the only significantly negative responses for both taxa/guild abundance and the cumulative effect measure (Table 3). However, these results should be viewed with caution as they are based on only 2 studies from the Northwest region (Hagar et al., 2004; Norton and Hannon, 1997) where birds were measured between 1 and 4 years post-treatment.

Breeding ($k=13$) and wintering ($k=3$) birds had similar responses to forest thinning both in magnitude and variation of effect sizes (Fig. 3). Wintering birds were only represented by three studies (2 in the Northwest and 1 in the Southeast). However, wintering bird diversity, taxa/guild, and cumulative effect sizes reported were significantly greater than 1.00 (Fig. 3). Of the thinning treatments included in the analysis, fuels treatment thinning had the most favorable effect on bird species abundance and diversity (Fig. 4). Neither precommercial nor commercial (non-fuels treatment) thinning effect sizes were significantly different from 1.00 (Fig. 4).

3.2. Discussion of bird response

Positive responses by many bird species to forest thinning have been well documented (Hayes et al., 1997, 2003; Hunter, 2001; Hagar et al., 2004; Kalies et al., 2010). Proposed mechanisms for increased abundance and diversity of bird species in thinned stands include increased regeneration and development of shrub and understory layers from greater light access to the canopy floor (Hayes et al., 1997) or increased horizontal or vertical variation in forest structure (McComb and Noble, 1980; Sullivan et al., 2002; Carey, 2003). Others have proposed that thinning can cause a more rapid return to conditions simulating older seral stages which in turn can increase number of species using the diversified habitat (Barbour et al., 1997; Bailey and Tappeiner, 1998).

Effect sizes significantly <1.00 occurred only for studies where >66% of basal area or trees per hectare were removed during thinning. Tree- and shrub-inhabiting birds may respond negatively to heavier thinning intensities (Norton and Hannon, 1997) or certain treatments or forest types (Christian et al., 1996). However, duration of time between thinning treatment and measurement of avifauna may play a substantial role in negative responses observed (Hagar et al., 2004; Greenberg et al., 2007a,b). Studies

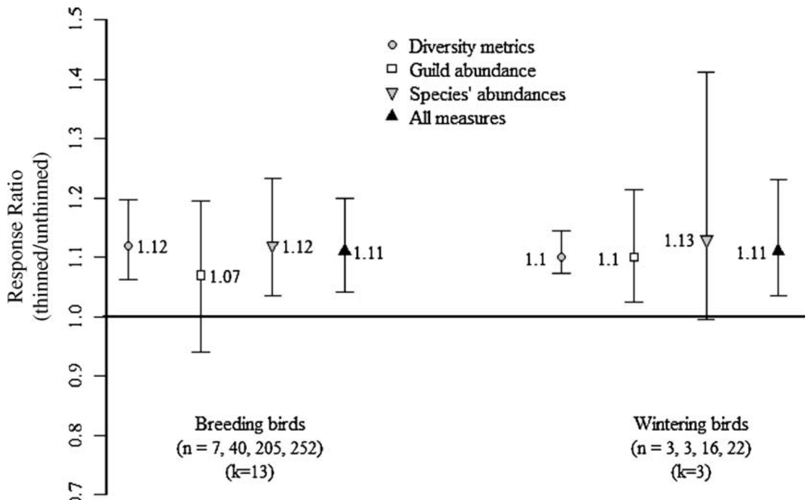

Fig. 3. Summary effect sizes for breeding and wintering birds across all treatments.

reporting negative avian responses to heavy intensity thinning observed bird species 1–2 years (Norton and Hannon, 1997) and 1–4 years (Hagar et al., 2004) post-treatment. As a result, any negative responses may be due in part to the short-term nature of the survey effort. Most thinning operations will have an initial short-term negative effect on biodiversity due to understory disturbance caused by the operation itself (Hagar et al., 2004). Response of the brown-headed nuthatch (*Sitta pusilla*) to thinning is immediate and positive, but other factors, such as number of snags, may ultimately determine their abundance (Wilson and Watts, 1999). Although diversity measures may often increase with thinning, consideration needs to be given to species of high conservation priority that may be negatively affected, either directly or indirectly, by thinning (e.g. Swainson's warbler (*Limnothlypis swainsonii*), brown creeper (*Certhia americana*) [Hayes et al., 2003; Bassett-Touchell and Stouffer, 2006]).

Across all methods of thinning harvest, fuels treatment thinning resulted in the largest effect sizes for birds suggesting a strong positive response for avian species diversity and abundance. In stands thinned as a fuels treatment, Siegel and DeSante (2003) found canopy, cavity and especially shrub-nesting avian species in higher abundance than in comparable unthinned stands. In drier forest types of the Southwest, removal of young conifer saplings and small trees in a fuels-treatment thin resulted in re-development of shrub growth and elevated densities of birds (Siegel and DeSante, 2003). In the Southeast, response to fuels treatment thinning appears to be influenced by treatment intensity, whether the thinning is followed with a burn, and which guild of birds species is being investigated (Greenberg et al., 2007a,b; Zebehazy et al., 2004).

4. Response of mammals to forest thinning

4.1. Results of mammalian species meta-analysis

We found 149 mammal responses (effect sizes) from 17 studies involving comparisons of thinned and unthinned forest stands (Table 1). There were more published mammal studies but fewer individual effect sizes than for birds. Measured effects came pri-

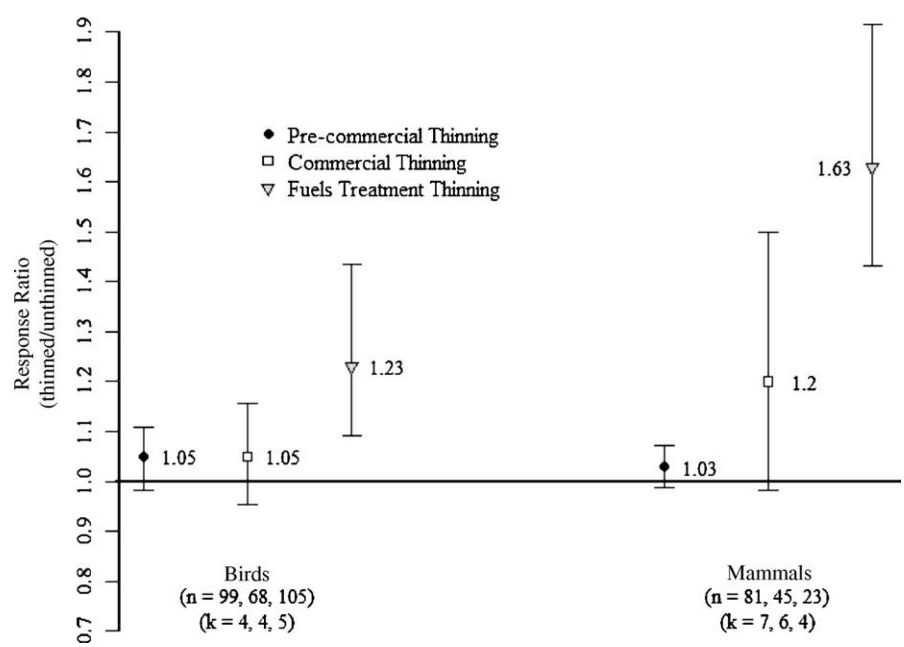

Fig. 4. Bird and mammal effect sizes for precommercial, commercial and fuels treatment thinning.

Table 3
Summary of effects of forest thinning on biodiversity by taxa and thinning intensity.[b]

	Light thin	Moderate thin	Heavy thin
Birds	$k=7$	$k=6$	$k=2$
Diversity	1.09 ($n=5$)[a]	1.13 ($n=4$)	1.37 ($n=1$)
Taxa/guild abundance	1.13 ($n=19$)[a]	1.19 ($n=17$)[a]	0.72 ($n=7$)[a]
Species abundance	1.08 ($n=104$)	1.18 ($n=92$)[a]	0.87 ($n=25$)
Cumulative	1.09 ($n=128$)[a]	1.18 ($n=113$)[a]	0.80 ($n=33$)[a]
Mammals	$k=8$	$k=9$	$k=6$
Diversity	1.50 ($n=1$)	1.02 ($n=4$)	1.03 ($n=5$)
Taxa/guild abundance	1.93 ($n=4$)[a]	1.37 ($n=7$)[a]	0.93 ($n=4$)
Species abundance	1.24 ($n=37$)	1.08 ($n=46$)[a]	1.08 ($n=41$)
Cumulative	1.31 ($n=42$)[a]	1.08 ($n=57$)[a]	1.06 ($n=50$)
Reptiles	$k=3$	$k=0$	$k=0$
Diversity	0.96 ($n=1$)		
Taxa/guild abundance	0.90 ($n=5$)	–	–
Species abundance	1.58 ($n=11$)[a]		
Cumulative	1.38 ($n=17$)[a]		
Amphibians	$k=2$	$k=2$	$k=2$
Diversity	0.98 ($n=2$)	–	–
Taxa/guild abundance	0.61 ($n=3$)	0.96 ($n=1$)	–
Species abundance	2.26 ($n=4$)	1.17 ($n=4$)	0.77 ($n=5$)
Cumulative	1.07 ($n=9$)	1.13 ($n=5$)	0.77 ($n=5$)
Invertebrates	$k=0$	$k=2$	$k=1$
Diversity		0.96 ($n=2$)	1.22 ($n=2$)[a]
Order/guild biomass	–	1.06 ($n=24$)[a]	1.21 ($n=18$)[a]
Species biomass		–	–
Cumulative		1.04 ($n=26$)	1.22 ($n=20$)[a]
All taxa combined	$k=16$	$k=16$	$k=9$
Diversity	1.12 ($n=9$)[a]	1.06 ($n=10$)	1.11 ($n=8$)
Taxa/guild abundance	1.16 ($n=31$)[a]	1.16 ($n=49$)[a]	0.85 ($n=29$)
Species abundance	1.09 ($n=156$)[a]	1.14 ($n=142$)[a]	1.02 ($n=71$)
Cumulative	1.10 ($n=196$)[a]	1.13 ($n=201$)[a]	0.99 ($n=108$)

[a] Indicates bootstrap confidence intervals (1000 iterations) did not include 1.00; k = # of studies, n = # of effect sizes.
[b] Determined by the percent of unthinned (control) stand basal area or trees per hectare remaining in thinned (treatment) stands (heavy: 0–33; moderate: 34–66; light: 67–100).

marily from studies of small mammals ($k=14$; $n=129$) but also included large herbivores (Sullivan et al., 2007) and bats (Tibbels and Kurta, 2003; Loeb and Waldrop, 2008). The deer mouse (*Peromyscus maniculatus*) was the most frequently reported individual species ($k=12$), with a significant cumulative effect size of 1.52.

Studies were available from all regions for the cumulative meta-analysis. Average timing of data collection from the 17 studies was 5.93 (±1.48) years post-thinning treatment. The number of effect size measures of mammalian taxa/guild abundance and diversity were somewhat limited, thus limiting conclusions based upon the meta-analysis. Mammalian diversity and abundance were higher in thinned stands than unthinned controls across most regions (Table 2). However, magnitude of the mammalian response to thinning treatments varied significantly between regions. Most studies were in the Northwest region (72%; $k=9$; Fig. 1), where there was no significant mammalian species abundance or diversity response to thinning treatments. All other regions, however, reported summary effects significantly greater than 1.00, suggesting a strong positive response of mammalian diversity and abundance to the variety of thinning treatments applied.

There was little difference in mammalian response by thinning intensity (Table 3). However, there was a gradual decrease in summary effect sizes reported (all were greater than 1.00) from light through heavy thinning intensities, with the latter being not significantly different from 1.00. Effect sizes for all 3 treatment types were above 1.00. Response of mammals to fuels treatment thinning was significantly greater than 1.00 and it was also significantly greater than measured mammalian response to precommercial thinning (Fig. 4).

4.2. *Discussion of mammal response*

Numerous studies have revealed a positive response of small mammals to forest thinning (Zwolak, 2009). Thinning is proposed to be beneficial to open-habitat and generalist small mammal species through increased light to and productivity of understory vegetation. Increased understory shrub and herbaceous vegetation increases forage and cover for deer mouse, jumping mice, and most vole species (Wilson and Carey, 2000; Suzuki and Hayes, 2003; Homyack et al., 2005), although response to the increase may be short-lived (Suzuki and Hayes, 2003).

In ponderosa pine forests of the Southwest (2–3 years post treatment), species responses to thinning treatments varied (Converse et al., 2006a), but total small mammal density was higher in thinned stands (Converse et al., 2006b). Bats are also typically favored by thinning operations across geographies through increased access to flying insects (Humes et al., 1999; Tibbels and Kurta, 2003; Loeb and Waldrop, 2008), but species-specific responses must be considered (Patriquin and Barclay, 2003). Thinning also often leads to no change in or increased densities of common small mammal species (Homyack et al., 2005). However, relatively little is known about influences of thinning intensity on response of small or large mammal populations (Suzuki and Hayes, 2003).

Although commercial thinning resulting in open canopies and increased understory growth may favor measures of mammalian species abundance or diversity, it may not improve habitat conditions for species associated with closed-canopy conditions (Lehmkuhl et al., 2002). However, intermediate or variable density treatments may produce habitat for generalists and closed canopy or arboreal specialists (Carey and Wilson, 2001; Lehmkuhl et al., 2002; Carey, 2003). As an example, Ransome et al. (2004) reported the lowest abundance of both northern flying squirrels (*Glaucomys sabrinus*) and American red squirrels (*Tamiasciurus hudsonicus*) in heavily thinned and unthinned lodgepole pine forests, whereas highest abundances were recorded in a moderate thinning treatment. Although typically associated with low intensity harvest, precommercial thinning has been shown to reduce small mammal species diversity in some instances (Etcheverry et al., 2005). However, precommercial thinning can lead to late-seral conditions developing at an earlier age, which may ultimately benefit species associated with older forests.

The thinning operation itself changes understory characteristics (e.g. prey availability, vegetative cover, and microclimate) that are linked to demographic parameters of many small mammals. As a result, thinning can initially have significant short-term effects on abundance and diversity of small mammals (both positive and negative) that do not persist (Greenberg et al., 2006, 2007a,b). Conversely, Garman (2001) reported a short-term influx of small mammals in thinned stands that disappeared beyond 3 years post-harvest. Our meta-analysis results confirm reported positive medium- and long-term response to forest thinning by mammals across all forest types and thinning intensities. Despite the generally positive response by mammals to forest thinning, some direct and indirect effects of forest thinning on species of conservation concern may warrant further review (e.g. northern flying squirrel habitat connectivity and food resources [Carey, 2000; Gomez et al., 2005] and snowshoe hare/Canada lynx population dynamics [Griffin and Mills, 2007; Hodges, 2000a,b; Homyack et al., 2007]).

5. Response of reptiles to forest thinning

5.1. *Results of reptilian species meta-analysis*

We found 17 reptile responses (effect sizes) from 3 studies in the southeastern U.S. (Table 1) (Kilpatrick et al., 2004; Todd and Andrews, 2008; Matthews et al., 2010). The cumulative effect size for 11 species abundance, 5 taxa/guild abundance and 1 diversity measure was 1.38 (Table 2). Twelve of 17 individual effect sizes reported were greater than 1.00.

5.2. Discussion of reptile response

Many reptile populations are potentially experiencing declines (Gibbon et al., 2000). However, research documenting response of reptiles to timber harvest is limited (Russell et al., 2004; Todd and Andrews, 2008). Solar radiation and thermal cover are important habitat characteristics for reptiles (Kiester, 1971). Standard clearcutting provides ample solar radiation for morning sunning, but may not provide adequate night time thermal cover in some regions. Thinning, on the other hand, may provide a more moderate environment for many reptile species than closed-canopy forest stands or recently clearcut stands (Todd and Andrews, 2008). Many lizard species, some of which have been reported in decline, have been shown to be in higher abundance on recently harvested stands (Greenberg et al., 1994; Kilpatrick et al., 2004).

The highest species richness and abundance of North American herpetofauna are in the southeastern U.S. (Kiester, 1971). The indication from available research (primarily from that region) is that forest harvest can variously affect reptile species depending on their life histories (Renken et al., 2004). However, more research would be required to draw conclusions about response to different thinning intensities and regional differences in reptile response to various thinning treatments.

6. Response of amphibians to forest thinning

6.1. Results of amphibian species meta-analysis

We found 19 amphibian responses from 5 studies; 2 in the northwestern U.S. (Garman, 2001; Suzuki, 2001), and 3 in the southeastern U.S. (Table 1) (Ford et al., 2000; Kilpatrick et al., 2004; Matthews et al., 2010). The cumulative effect size for all abundance and diversity measures was 0.94, but was not significantly different from 1.00 (Table 2). However, the cumulative taxa/guild abundance effect size (0.95) was significantly less than 1 (Table 2). Suzuki (2001) and Matthews et al. (2010) reported lower total amphibian abundance in thinned stands than unthinned stands. Twelve of 19 reported effects were less than 1.00.

Fowler's toad (*Bufo fowleri*), eastern narrow-mouthed toad (*Engystoma carolinense*) (Kilpatrick et al., 2004) and Ensatina (*Ensatina eschscholtzii*) (Garman, 2001) had the strongest positive responses to forest thinning. The Ensatina (incl. all subspecies) was the only species measured in different thinning intensities and studies (Garman, 2001; Suzuki, 2001). Suzuki (2001) found slightly lower abundances of Ensatina in thinned stands than unthinned control stands 1–2 years post-harvest. Conversely, Garman (2001) measured Ensatina response to thinning treatments between 5 and 8 years post harvest and found a strong positive effect of moderate and heavy thinning intensities.

6.2. Discussion of amphibian response

Salamanders represented 11 of 19 effect sizes used to summarize amphibian response to thinning. Salamanders, particularly plethodontid salamanders, are often more abundant in closed-canopy forests and later successional stages (Corn and Bury, 1989; Ash, 1997; Aubry, 2000; Semlitsch et al., 2009). Declines of up to 80% for some salamanders and species richness declines of up to 50% have been reported following even-age timber harvest in some forest types (Petranka et al., 1993). In a comprehensive review of amphibian response to forest management in North America, deMaynadier and Hunter (1995) report the short-term, stand-level response of salamanders to timber harvest is typically negative, especially for clearcutting, usually through the mechanisms of reduced leaf litter, canopy cover and soil moisture (deMaynadier and Hunter, 1995; Pough et al., 1987; Ash, 1997; Semlitsch et al., 2009). Pough et al. (1987) showed a strong linear relationship of understory vegetation and leaf litter depth with above-ground salamander activity, and Ash (1997) reports the timing of amphibian return to previously harvested stands closely follows re-development of the litter layer.

Less information is available on amphibian response to partial harvest or thinning. Some suggest that detrimental effects of stand disturbance (e.g. soil compaction, stream sedimentation) on amphibian populations persist even when the disturbance is a less severe partial cut (Harpole and Haas, 1999; Semlitsch et al., 2009). However, Brooks and Kyker-Snowman (2008) found forest floor temperature and humidity to be similar between partial, selection-based timber harvests and unharvested control stands. Several studies report mixed or even positive effects of thinning on amphibian populations (Pough et al., 1987; Grialou et al., 2000; Renken et al., 2004; McKenny et al., 2006) suggesting that thinning harvests can maintain forest amphibian populations. In a study comparing thinning with riparian buffers to unharvested control stands, Kluber et al. (2008) found no treatment effect across 7 species of amphibians. The less extreme response to thinning (when compared to even-aged regeneration harvests) by the understory and forest litter layers may explain the more moderate, short-term amphibian response to thinning when compared to even-age stand management (Petranka et al., 1993). Enhanced productivity of herbaceous and shrub forest understory also can create favorable soil moisture conditions for amphibian species (Zheng et al., 2000).

Although increasing numbers of studies in managed forest settings have focused on amphibians (Russell et al., 2004; Kroll, 2009), we found few reporting the experimental results needed for meta-analysis. Nevertheless, the studies we evaluated, and the lack of significant response, suggest the biophysical characteristics necessary for moisture sensitive amphibian species may still be retained in thinned forests (Ford et al., 2000).

7. Response of invertebrates to forest thinning

7.1. Results of invertebrate species meta-analysis

We found 46 invertebrate responses (effect sizes) from 2 studies; 1 in the northwestern U.S. (Yi, 2007), and another in the upper Midwestern U.S. (Table 1) (Tibbels and Kurta, 2003). Thinned stands reported significantly higher biomass of invertebrates than unthinned stands for 35 of 42 order biomass effect sizes. The cumulative effect size of 1.10 for 42 order biomass measures and 4 measures of order diversity was significantly greater than 1.00 (Table 2). Response magnitude was similar for both studies.

7.2. Discussion of invertebrate response

Insects are affected in a variety of ways by changes to the forest canopy, understory, and litter layers, and can themselves be significant drivers of forest productivity and nutrient cycling (Hunter, 2002). The diversity of arthropod functional groups can be a good measure of overall habitat complexity (Hunter, 2002; Yi, 2007). However, effects of forest thinning on invertebrates are not well understood (Duguay et al., 2000; Schowalter et al., 2003; Yi, 2007). Mechanisms for the increase or decline of certain invertebrates in response to forest thinning are often specific to the functional group being examined. Some examples include increases in abundance of herbivorous arthropods in recently thinned stands due to increased availability of canopy level forage and declines in populations of detritovores and some predators due to reduced habitat

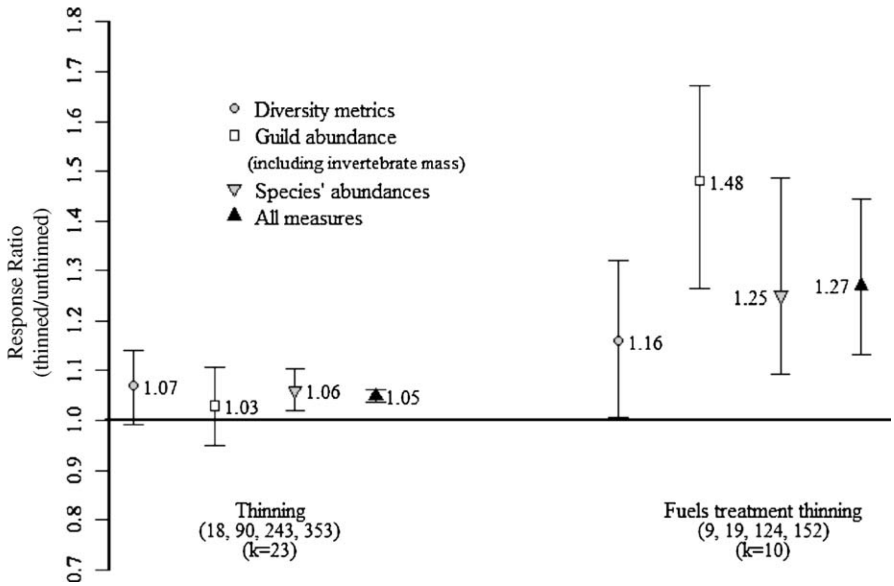

Fig. 5. Summary effect sizes for standard thinning and fuels treatment thinning across all taxa.

and food resources (Progar et al., 1999). Thinning that changes the community composition and structure of understory vegetation can increase diversity and abundance of some insect groups in the short term (Taki et al., 2010).

Depending on their life history characteristics, invertebrate communities have been shown to respond positively (Yi, 2007), negatively (Niemela et al., 1993), or minimally (Schowalter et al., 2003; Apigian et al., 2006) to forest thinning and other canopy-opening disturbances. The research we summarized, including responses for several different types of arthropods (i.e. herbivores, predators, detritovores), demonstrated a significant positive summary response to forest thinning treatments. However, our results are limited in geographic scope and in the number of reporting studies.

8. Fuels treatment thinning

Excessive fuel loading in stand understories has become a significant issue especially in regions with historically frequent fire return intervals that have been altered through suppression (Waldrop et al., 2004). As a result, forest biomass removal harvest to reduce fuel loads will likely continue to occur especially throughout forests in the western U.S. (USDA Forest Service, 2005; Evans and Finkral, 2009). Fuels treatment thinning is distinct from other types of thinning, not only in its selective regional application and limited potential for economic gain, but in the intensity of disturbance. For that reason, we offer separate discussion of the response of diversity and species abundance to fuels treatment thinning.

Thinning intensity in 7 of the 10 fuels treatment studies was considered light (0–33% of the basal area removed), the remainder, were of moderate intensity (34–66% basal area removed). Our results show that studies of fuels treatment thinning had significantly higher taxa/guild abundance and cumulative effect sizes than non-fuels treatment thinning experiments (Fig. 5). Across 152 effect sizes of fuels treatment thinning, abundance, and diversity measures were higher in fuels treatment thinned stands than unthinned (control) stands (Fig. 5). Proposed mechanisms for this substantial increase in abundance and diversity are similar to those for precommercial thinning and include increases in forest productivity, reduced competitive dominance, and redevelopment of the understory shrub and herbaceous layers. The differences in magnitude of response for fuels treatment versus precommercial thinning may be due to forest type and regional differences as much as the treatment itself.

Some concerns with widespread application of fuels treatment thinning still remain. Mechanical fuels treatment thinning will typically result in fewer snags than a prescribed burn or thin/burn treatment (Greenberg et al., 2007a,b). In addition, soil compaction from increased stand entries could occur, although reducing the number of skid trails would likely reduce the potential for this impact (Moghaddas and Stephens, 2008). However, our analysis and other research (Converse et al., 2006a,b) suggest at the very minimum, short-term gains for total mammal abundance, species diversity and forest health after fuels treatment thinning.

9. Effect of forest thinning on plant species diversity

The response of plant species diversity to forest thinning is often positive, but has been less studied than faunal diversity (Halpern and Spies, 1995; Thomas et al., 1999). In the northwestern U.S. and Canada, species richness of understory vegetation in thinned stands was similar to (Deal, 2001) or greater than (Thomas et al., 1999) uncut control stands. In structurally complex temperate rain forests of the northwestern U.S., thinning increased growth of important mid-canopy layers (Comfort et al., 2010). Lodgepole pine forests of the Northwest Interior exhibited few differences in plant species diversity or composition between thinned and unthinned stands (Sullivan et al., 2002). In boreal forests, the peak plant species richness occurred in early seral stages. As forest succession continued, precommercial thinning sustained high levels of plant diversity (Weidenfalk and Weslien, 2009).

Plant species richness in ponderosa pine forests of the southwestern U.S. was least in unmanaged stands and increased with greater thinning intensity (Griffis et al., 2001). However, exotic species were a large part of the increase in richness for harvested stands, and number of native shrub species decreased significantly with treatment intensity (Griffis et al., 2001). In Sierran mixed conifer forests, canopy closure, used as a measure of thinning intensity, was shown to be negatively related to plant species richness (Battles et al., 2001). In addition, plant species composition varied significantly with intensity of thinning treatments. High intensity treatments maximized species richness but understory vegetation typical of late seral stands was more abundant in lightly thinned or control stands. Furthermore, control stands had lower proportions of exotic species (Battles et al., 2001). By 3 years post-treatment, thinned stands showed significantly higher plant species richness than control stands in the Piedmont of South Carolina (Phillips and Waldrop, 2008).

In summary, the response of plant species diversity to forest thinning across much of North America is likely to be positive, but will depend on the forest type and treatment intensity. Plant species composition and abundance of exotic species are also likely to vary with thinning intensity.

10. Summary of biodiversity effects and management implications

Though harvesting live trees for biofuels production as part of a sustainable forest management program disturbs ecological processes to some extent, such disturbances do not negatively affect biological diversity in most cases (Janowiak and Webster, 2010). Our results show that, across most thinning intensities and forest types, thinning adds to the abundance and diversity of a variety of taxa. The magnitude of response to forest thinning, either positive or negative, is often small. It is important to recognize that some species of higher conservation concern may be either positively or negatively affected by thinning and that simple diversity and richness measures may not be sufficient for fully understanding the effects of thinning on biodiversity. Furthermore, thinning (as with any silvicultural practice) is not implemented simultaneously across the landscape. As a result, biomass thinning harvest across a range of intensities will likely result in increased species abundance and diversity in most forest types.

Disturbance can increase species diversity at stand and landscape scales by creating a variety of habitat types through a mosaic of forest development stages (Hunter, 1999; Franklin et al., 2002; Loehle et al., 2002; Lindenmayer et al., 2006). However, species response to disturbance can depend on biophysical setting of the landscape (McWethy et al., 2010). In highly productive systems with lengthy inter-disturbance periods, a few species can begin to dominate the community, leading to reduced levels of diversity (Huston, 1999, 2004; Odion and Sarr, 2007). Forest thinning for biofuels production in highly productive forests may provide the disturbance necessary to counteract competitive dominance. Alternately, in less productive forests, more care may be required to blend objectives for biomass harvest with those for maintenance of biological diversity (Janowiak and Webster, 2010; Page-Dumroese et al., 2010). Disturbance intensity and biophysical setting are likely to be strong determinants of response by wildlife and vegetation to biomass thinning harvests (Greenberg et al., 2007a,b). Thinning designed to promote species diversity will likely need locally tailored prescriptions of intensity and pattern (Hagar et al., 2004).

Forested regions of North America harbor a significant proportion of the total terrestrial biodiversity (Hansen and Rotella, 1999). Much of this land is privately owned and is under increasing pressure from rural residential development (Huston, 2005; Gude et al., 2006). Thinning for biofuel production may offer land managers an additional economic incentive to retain their ownership in forest cover and the opportunity to address other silvicultural and ownership objectives (Page-Dumroese et al., 2010). However, stand accessibility, terrain, transportation costs, and availability of processing plants are just a few of the factors that will influence long-term viability of thinning for biofuels production (USDA Forest Service, 2005).

11. Geographic limitations, empirical knowledge gaps and research needs

The meta-analysis we completed for reptiles and amphibians suffers from a limited number of studies and non-uniform geographic distribution of results. Few meaningful conclusions should be drawn from the meta-analysis of reptile responses originating from only 3 published studies in the Southeast. Many of the responses included in this analysis were of abundance measures for single species. However, abundance is not always related to habitat quality and may only reflect short-term occupancy of the sampled stand (Van Horne, 1983). Furthermore, as a result of common species being disproportionately included due to the availability of data, analysis of single species responses may or may not provide an accurate picture of biodiversity response (Lennon et al., 2004; Prendergast et al., 1993).

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